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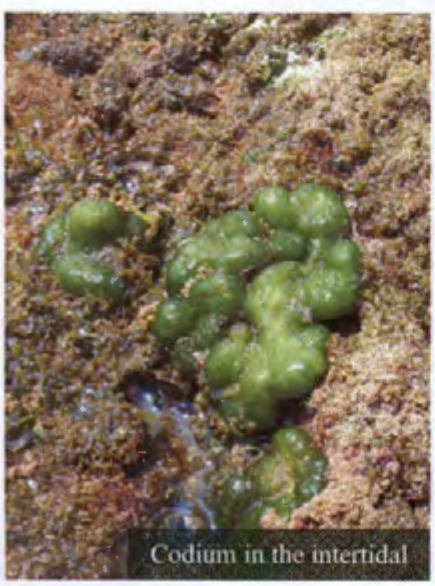
Tropical intertidal seaweed turf communities of Jesser Point, Sodwana Bay, South Africa

Jesser Point, Sodwana Bay



Codium in the intertidal

25 x 25 cm quadrat on the low shore

Abstract

Algal turfs play an important role in both tropical and temperate reef ecology, supporting a diverse array of macrofauna as well as being primary producers within both intertidal and subtidal ecosystems. Biodiversity and biomass patterns of the intertidal algal turfs at Sodwana Bay, South Africa have not yet been established so this study was undertaken to investigate these. It was hypothesised that both biodiversity and biomass would decrease with increasing height along the shore, as well as that sediment would have an effect on the community composition of the turfs. The community was sampled over a vertical range of 1.2 m and found to be dominated by the red alga *Jania intermedia* (24.21 % of total algal coverage) followed by *Tolypiocladia glomerulata* (18.05 %), *Dictyota sp.* (13.39 %), *Jania adhaerens* (12.32 %) and *Sphacelaria tribuloides.* (5.83 %). No significant vertical zonation patterns were found, though certain species showed vertical trends such as *Asparagopsis taxiformis* and *Sphacelaria tribuloides*, which occurred in greatest biomass lower down on the shore, while *Tolypiocladia glomerulata* occurred higher up on the shore. Sand was found to affect certain species more than others, with *Tolypiocladia glomerulata*, *Jania adhaerens* and *Asparagopsis taxiformis* occurring in greatest biomass when the amount of sediment found in the quadrat was low, while *Sphacelaria tribuloides*. showed the opposite pattern and *Jania intermedia* showed no distinct pattern. Sampling took place over 1.2 m vertical height along the shore at spring low tide therefore covering 60 % of the intertidal zone vertically (maximum tidal range in South Africa is 2 m). It is therefore possible that the turfs are the cause of a decline in zonation by remaining damp and decreasing desiccation gradients vertically along the shore.

Introduction

Algal turfs play an important role in both tropical and temperate reef ecology (Klumpp & McKinnon 1989) and tend to dominate reef flats and shallow intertidal habitats in both tropical and temperate regions all over the world (Hay 1981, Klumpp & McKinnon 1989). Algal turf is defined as a low-standing (> 1 cm high) crop of erect macroalgae (Klumpp & McKinnon 1989, Coleman 2002) that covers extensive areas of the substrate (Coleman 2002; Copertino et al. 2005), forming thick, dense mats of biomass (Hackney et al. 1989; Stuercke & McDermid 2004; Copertino et al. 2005; Kelaher 2005; Carpenter & Williams 2007; Miller et al. 2009). Adaptive advantages to the turf growth form have caused convergent evolution in the three major seaweed divisions (Rhodophyta, Chlorophyta and Phaeophyta) (Hay 1981) though Cyanophyta are also found within turf assemblages and turf assemblages often form in close association with microscopic and epiphytic algae (Anderson et al 2005).

Turfs are both dynamic (Coleman 2002) and highly diverse, multispecific assemblages (Stuercke & McDermid 2004; Anderson et al. 2005; Copertino et al. 2005; Carpenter & Williams 2007; Wallenstein et al. 2009), showing substantial morphological plasticity (Hay 1981; Miller et al. 2009) as well as a high biomass turnover rate of once every 4 – 12 days (Klumpp & McKinnon 1989; Copertino et al. 2005). This rapid growth rate allows for, and is thought to be an adaptation to, resilience against biological and environmental stresses (e.g. grazing pressure, desiccation stress and intense wave action; Hay 1981; Klumpp & McKinnon 1989; Hackney et al. 1989, Wallenstein et al. 2009) thereby allowing turfs to have a competitive advantage in high stress zones (Cruz-Motta 2007; Liuzzi & Gappa 2008; Miller et al. 2009; Prathep et al. 2009; Wallenstein et al. 2009). These dense mats of algal turf play a very important role in intertidal ecosystems because they support a plethora of other macroorganisms both faunal and floral (Stuercke & McDermid 2004; Kelaher 2005; Copertino et al. 2005; Huff & Jarett 2007), that would otherwise be unable to survive in areas exposed to high biological or environmental stress (Liuzzi & Gappa 2008). This occurs to such an extent that previous reports have labelled algal turfs as both ecosystems in their own right (Wallenstein et al. 2009) and autogenic ecosystem engineers (Liuzzi & Gappa 2008). Seaweed turfs contribute significantly to reef primary productivity (Adey & Goertemiller 1987; Hackney et al 1989; Stuercke & McDermid 2004; Carpenter & Williams 2007; Copertino et al. 2009), contributing up to 70-80 % of productivity on coral reefs (Hackney et al. 1989). Higher surface to volume ratios often result in turfs having a greater mass-specific productivity than larger foliose macroalgae (Miller et al. 2009), though some turf-forming species have been shown to be more productive outside the turf habitat (Hay 1981; Miller et al. 2009). On temperate reefs and in foliose macroalgal assemblages, however, it is the foliose macroalgae that are the greatest producers (Miller et al. 2009).

The effects of sedimentation on shallow marine ecosystems have been widely studied, especially on rocky shore systems (e.g. Littler et al. 1983; Littler et al. 1991; Engledow & Bolton 1994; Renaud et al. 1996; Airoldi & Cinelli 1997; Huff & Jarrett 2007; Yanez et al. 2008). It is generally agreed that sedimentation, while detrimental to some species such as canopy-forming macroalgae (Airoldi & Cinelli 1997; Ortega-Borges et al. 2009), as well as possibly to biodiversity through exclusion of less tolerant species (Engledow & Bolton 1994; Airoldi & Cinelli 1997) may have positive effects on the biodiversity of shallow marine ecosystems through preventing monopolisation of an area by competitively advantaged species (Airoldi & Cinelli 1997; Yanez et al. 2008; Ortega-Borges et al. 2009). This, however, is only true to an extent, as excessive sedimentation has been shown to be detrimental to biodiversity by means of elimination of opportunistic and even tolerant species if the sedimentation is too great or too prolonged (Yanez et al. 2008). This may happen by means of smothering and deprivation of light and oxygen to the organisms in the system (Littler et al. 1983;

Schiel et al. 2006), or by means of excessive sediment movement by strong wave action, which may scour or abrade the environment (Littler et al. 1983; Schiel et al. 2006), sometimes to the point of removing whole organisms from the substrate (Yanez et al. 2008; Schiel et al. 2006). Sedimentation can therefore be called a major driver of coastal marine diversity (Balata et al. 2007). Sediments and sedimentation are now considered to be a structural constituent of algal turf (Airoldi & Cinelli 1997) and have a direct effect on both algal turf recruitment and growth rates (Airoldi & Cinelli 1997; Prathep et al. 2003). Balata et al. (2007) found that turf algae actually proliferate under heavy sediment loads, but Airoldi & Virgilio (1998) found that turf responses to sedimentation vary with differing spatial scales and co-depend on various other factors both physical and biological. The presence of algal turf has both direct and indirect effects on other colonising organisms such as foliose macroalgae and benthic macrofauna, meaning that variations in sedimentation rates may affect, indirectly, the local diversity of benthic assemblages (Airoldi & Cinelli 1997; Prathep et al. 2003; Mei & Schiel 2007) through changes in recruitment and growth rates of turf algae (Airoldi & Cinelli 1997). Algal turfs also indirectly influence sedimentation rates locally by trapping sediment through the reduction of water flow in the boundary layer causing deposition of sediment (Prathep et al. 2003; Birrell et al. 2005; Mei & Schiel 2007; Logan et al. 2008).

Humans are currently having a substantial effect on sedimentation rates, especially on human-dominated coasts through coastal manipulations such as the building of harbour walls, beach replenishment and sand dredging (Balata et al. 2007; Schiel et al. 2006; Huff & Jarett 2007). This is just one of the many effects anthropogenic activities are having on coastlines worldwide, with others including coastal pollution due to nutrient runoff from agriculture and/or sewage works (Russell et al. 2009); coastal exploitation and removal of key species (Edwards & Estes 2006); and the effects of global climate change, including temperature fluctuations and ocean acidification (Martin & Gattuso 2009), all of which potentially result in changes at all scales (Kuffner et al. 2008; Connell & Russell 2010; Hurd et al. 2010). Anthropogenic impacts on coastal systems are beyond the scope of this project and will not be one of my focuses, however for further reading on these consult Guinotte & Fabry (2008); Walker et al. (2008); Russell et al. (2009) .

Sodwana Bay lies on the east coast of South Africa, along the northern coast of KwaZulu Natal (KZN), approximately 70 km south of the Mozambique border (Anderson et al. 2005). The northern KZN continental shelf is narrow (Ramsay & Mason 1990; Ramsay 1994; Ramsay & Miller 2006) - approximately 3 km wide (Ramsay & Mason 1990) when compared to the global mean of 75 km wide (Ramsay & Miller 2006), allowing the warm Agulhas Current - the dominant oceanographic feature of this coastline formed by the confluence of surface waters in the Mozambique channel (Ramsay 1994) -

to flow close inshore (Ramsay & Mason 1990). Sodwana Bay is a tropical region, with mean monthly sea temperatures ranging between 21 °C and 28 °C at a depth of 18 m (Schleyer et al. 2008), and between 18 °C and 29 °C at the surface (Anderson et al. 2005). The area is situated within the Indo-West Pacific biogeographic realm (Sink et al. 2005). The coastline in this area has a tidal range of approximately 2 m (Ramsay & Mason 1990) and is dominated by high-energy waves and swells from the southeast, which result in a net northward longshore drift (Ramsay & Mason 1990). Late Pleistocene sediments are present along the northern KZN coastline in the form of aeolianite/beachrock reef complexes. These consist of carbonate-cemented dune or beach sands, which formed during sea-level lowstands during the Pleistocene (Ramsay & Miller 2006) and many now form marine platforms which are exposed during low tide (Anderson et al. 2005), as is the case with Jesser Point, the study site used in this paper.

In a previous study done on the tropical subtidal algal turfs of Sodwana Bay (Anderson et al. 2005) it was found that both seaweed diversity and total seaweed biomass decreased with depth (0.5 m – 29.0 m) and that sediment had a significant effect on seaweed communities, but showed no pattern with depth. The aim of this experiment is to determine the same basic diversity and biomass patterns vertically along the lower intertidal zone as well as to determine whether sedimentation has an effect on the turfs present or their coexisting fauna. The hypotheses proposed were that 1) seaweed turf diversity will decrease with increasing height on the shore as a result of desiccation stress; 2) seaweed biomass will decrease with increasing height on the shore due to desiccation stress; 3) sediment will affect the turfs and/or the coexisting fauna found along the shore; and 4) benthic fauna as well as grazers will have an effect on seaweed turf biomass and diversity. Visual observation indicates a decrease in seaweed biomass with increasing height on the shore as turfs are found mostly in areas below the barnacle zone, with some *Gelidium* turf seen in the barnacle zone and *Ulva*- and cyanobacteria found on the upper shore. Whether the same is true for biodiversity is yet to be determined, though logic would dictate that with increased height on the shore comes increased desiccation, thereby allowing only desiccation-adapted species to survive higher up the shore. Also predicted is that fine sand may have a negative effect on the fauna such as grazers and filter feeders through the clogging of their filter feeding apparatus (Schiel et al. 2006), thereby decreasing herbivory stress to the seaweeds, causing increased biomass (and possibly diversity) in areas exposed to greater volumes of fine sediment.

Methods

Study site and sampling

Jesser point is an approximately 1 km stretch of fossilised dune rock outcropping situated along the coast of Sodwana Bay at GPS co-ordinates 27°32'23.9"S 32°40'47.7"E (Figure 1). Distances between Jesser Point and adjacent dune rock outcroppings are approximately 11 km to the north and 9 km to the south. The focus of our study was on the northernmost and highest point of the outcropping, which extends from the intertidal down into the subtidal, where it is almost continuous with Quarter-Mile Reef. The outcropping has a relatively shallow slope with large expanses of bare rock and little biodiversity seen along the top of the shore. Raised barnacle platforms are seen approximately halfway down the shore in the mid-eulittoral zone, followed by flatter expanses of rock covered in algal turfs as well as other intertidal organisms such as tubeworms, limpets, reef worms and mussels. Pothole-like pools are found at all heights on the outcropping. Algal turfs are found mostly on the lower shore (below the barnacle platforms), though some turfs are found in amongst the barnacles, such as *Gelidium* and *Ralfsia*, as well as some on the high shore such as *Ulva*- and cyanobacteria.

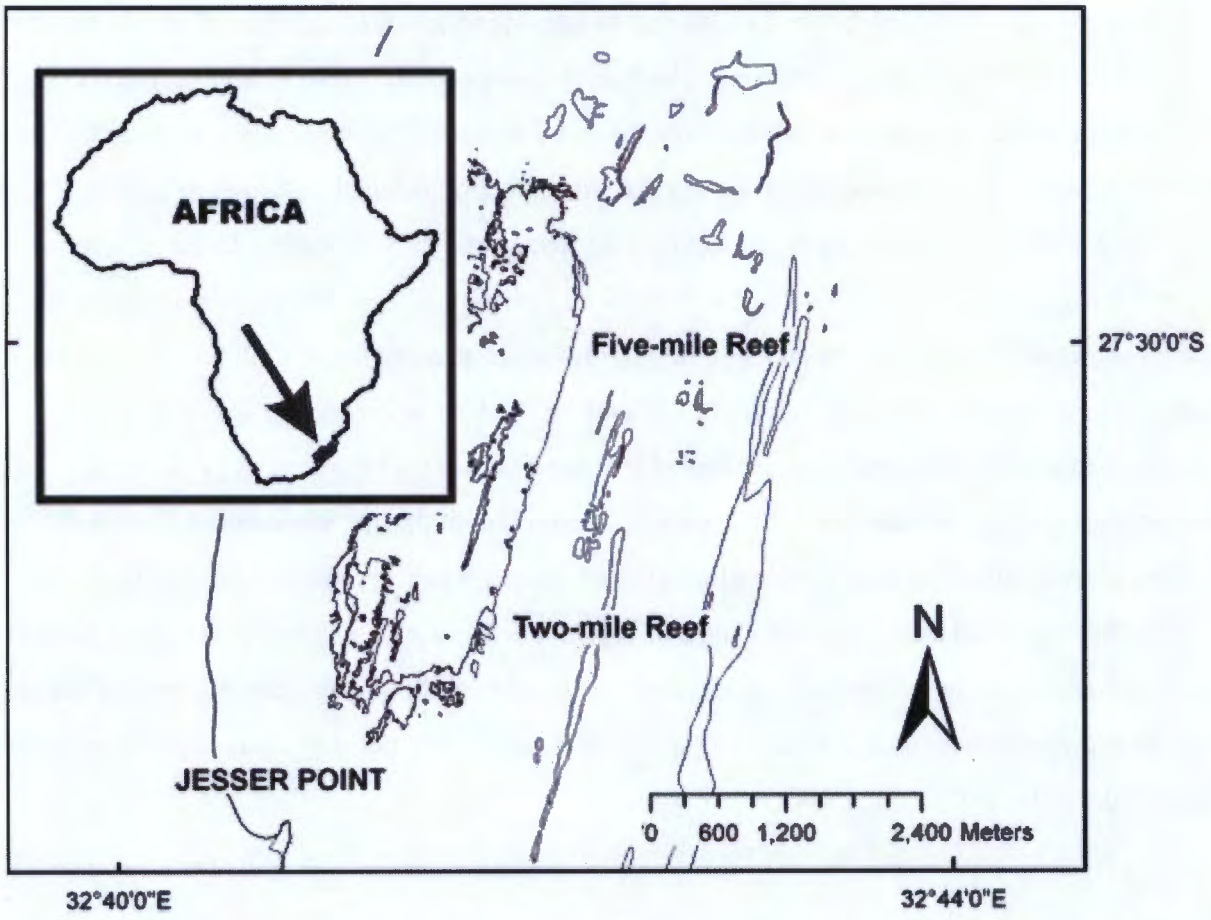


Figure 1. Illustration of the study site Jesser Point, Sodwana Bay, South Africa. Adapted from Schleyer et al. (2008)

Sampling took place between the low spring tide level and the barnacle zone as turfs mostly occurred in this area. All sampling took place in February 2010 (late summer); meaning that no seasonal changes were investigated though seasonality may play a role in community composition. Sampling took place over a vertical distance of 1.2 m, ranging from the spring low tide level to the barnacle zone, which occurred between 1.5- and 2 m above Chart Datum. The maximum tidal range in South Africa is ~2 m (Schumann & Orren 1980), therefore microtidal or low mesotidal (Ramsay & Mason 1990), meaning that all sampling occurred below the high water mark. Five transects, each consisting of between four and six 25 cm x 25 cm quadrats, were sampled. The transects were chosen subjectively, with areas of high turf density chosen over areas with little or no turf coverage. Transects were between 5 and 20 m apart and ranged between 3- and 15 m in length. Sampling took place during spring low tide so as to get maximum intertidal coverage. Quadrats were placed at equidistant intervals along each transect and all organisms found within each quadrat were removed from the substrate using a paint scraper. Samples were placed in labelled plastic bags with sea water for sorting later the same day. Accurate distances between quadrats as well as height above tide level were measured using a laser levelling device (Skil Ranger ®) and metre rule. The theoretical height above Chart Datum on each day was noted and the height of the lowest sample above sea level at low tide was measured, in order to calculate the vertical height of each quadrat above Chart Datum.

Sorting and identification

Samples were sorted into plant and animal matter, with animal matter including worm tubes (both reef worm and tubeworm), barnacles, limpets and mussels upon which turf was growing. Animal matter was wet-weighed separately so as to determine animal proportions within each quadrat. Once the algal and animal matter had been removed from the sample the sample was sieved to separate out the sand obtained in each sample. Wet weights of the sand from each sample were obtained following manual squeezing out of the water, in order to determine whether sand was playing a role in both animal and turf habitats. Animal and sand data were recorded for ecological analysis. The algal matter was preserved in a 5 % formalin in seawater solution and stored in the dark for subsequent identification.

Samples taken from each quadrat were sorted using a dissecting microscope (Leica) at 8X magnification and permanent slides were made of all taxa found in each sample. Where the specimen was too large for a slide it was placed in a separate small container with 5 % formalin in sea water for subsequent identification. Permanent slides were made using a karo syrup-based solution (75 % Light karo syrup, 21 % distilled water, 2 % Phenol crystals, 2 % Formalin [33 % Formalin in seawater]). Ecological algal abundance data were obtained by examination of a sub-sample taken from each quadrat sample under a dissecting microscope to determine the percentage cover of each species found

within each sample. Samples were wet-weighed for determination of mass contributions of each species. Slides were examined using a compound microscope (Leica) at 40X or 100X magnification (depending on the size of the specimen), in order to identify each specimen down to genus level, or to species level where possible.

Analysis

Ecological algal abundance percentage cover data were converted to mass data for analysis. Data were separated into height classes of 20 cm between 1 cm and 120 cm, and sorted according to each quadrat's height above Chart Datum (CD). SIMPER analyses (PRIMER 6) were performed on the algal species data, which were factored by a) transect and b) height class for analysis, in order to determine Bray-Curtis similarities between quadrats as well as dissimilarities between transects and height classes. ANOSIM (PRIMER 6) analyses were then performed using the same factors.

Graphs of biomass of the six most important species contributing to similarities and differences between and amongst transects, height classes and quadrats were plotted against height above CD (Figure 4) in order to obtain an idea of their vertical shore distribution, as well as against amount of sediment as mass (Figure 5) in order to determine species-sediment relationships.

Canonical Correspondence (CANOCO) (ECOM: Pisces Ltd.) analyses were performed on the algal species data as well as on the algal species data combined with faunal mass data (algal plus animal data) in order to determine effects of the present fauna on the algal species. Correlation analyses using sites at species centroids were performed on the algal species and the algal plus animal species data, with height above CD (height) and amount of sediment (sand) as environmental factors.

Average linkage cluster analyses (CAP 4) using Euclidean Distance were then performed on the algal species and algal plus animal species data along with MDS plots (CAP 4) using Bray-Curtis, in order to obtain visual representations of similarity and clustering. Species richness was then calculated for each quadrat and a multiple regression (STATISTICA 8) was performed to determine the relationship between height above CD, amount of sediment and species richness.

Departures from normality in the species richness, height above CD and amount of sediment data (separately) prevented the use of ANOVA. Instead, nonparametric Kruskal-Wallis Multiple Comparisons analyses were performed on the three data sets to determine significant differences in species richness, height above CD and amount of sediment between both transects and height classes.

Results

Figures 2 and 3 illustrate the total mass each species contributed to the total algal mass collected across the study site, separated into Transect and Height Class stacks respectively. Figure 2 also shows species contributions as a percentage indicated above each column. Quantitatively the study site was dominated by the articulated red alga *Jania intermedia* (Kützing) P.C. Silva, which contributed 24.21 % of the total algal mass collected, followed by *Tolypiocladia glomerulata* (C. Agardh) F. Schmitz (18.05 %), *Dictyota sp.* (13.39 %), *Jania adhaerens* J.V. Lamouroux (12.32 %) and *Sphacelaria tribuloides* Meneghini (5.83 %). Species contributions greater than 50 g follow in Table 2.

Table 1. Species names and abbreviations used in text and results.

Species	Abbreviation
Jania intermedia (Kützing) P.C. Silva	JIN
Tolypiocladia glomerulata (C. Agardh) F. Schmitz	TCL
Dictyota sp.	DCT
Jania adhaerens J.V. Lamouroux	JAD
Sphacelaria tribuloides Meneghini	SCL
Chondria sp.	CND
Cyanobacteria	BG
Asparagopsis taxiformis (Delile) Trevisan de Saint-Léon	AGS
Codium arabicum Kützing	CDAR
Valonia macrophysa Kützing	VLN
Hypnea sp.	HPN
Gelidiella sp.	GLD
Pteracladiella sp.	PCD
Lobophora sp.	LBP
Polysiphonia sp.	PSP
Rhizoclonium grande Børgeson	RZCG
Codium acuminatum O. Schmidt	CDAC
Laurencia sp.	LRC
Caulerpa sp.	CLP
Ceramium sp.	CRM
Ectocarpoid species	ECP
Centroceras sp.	CTC
Ralfsia sp.	RFS
Tubeworms	TWM
Barnacles	BNC
Reef Worms	RWM
Limpets	LMP
Mussels	MSL

Table 2. Species contributing >50 g mass to total algal mass collected across the entire study site.

Species	Mass Contribution (g)
Jania intermedia	321.8
Tolypiocladia glomerulata	239.9
Dictyota sp.	178.0
Jania adhaerens	163.7
Sphacelaria tribuloides	77.5
Chondria sp.	58.4
Cyanobacteria	53.2
Asparagopsis taxiformis	52.4

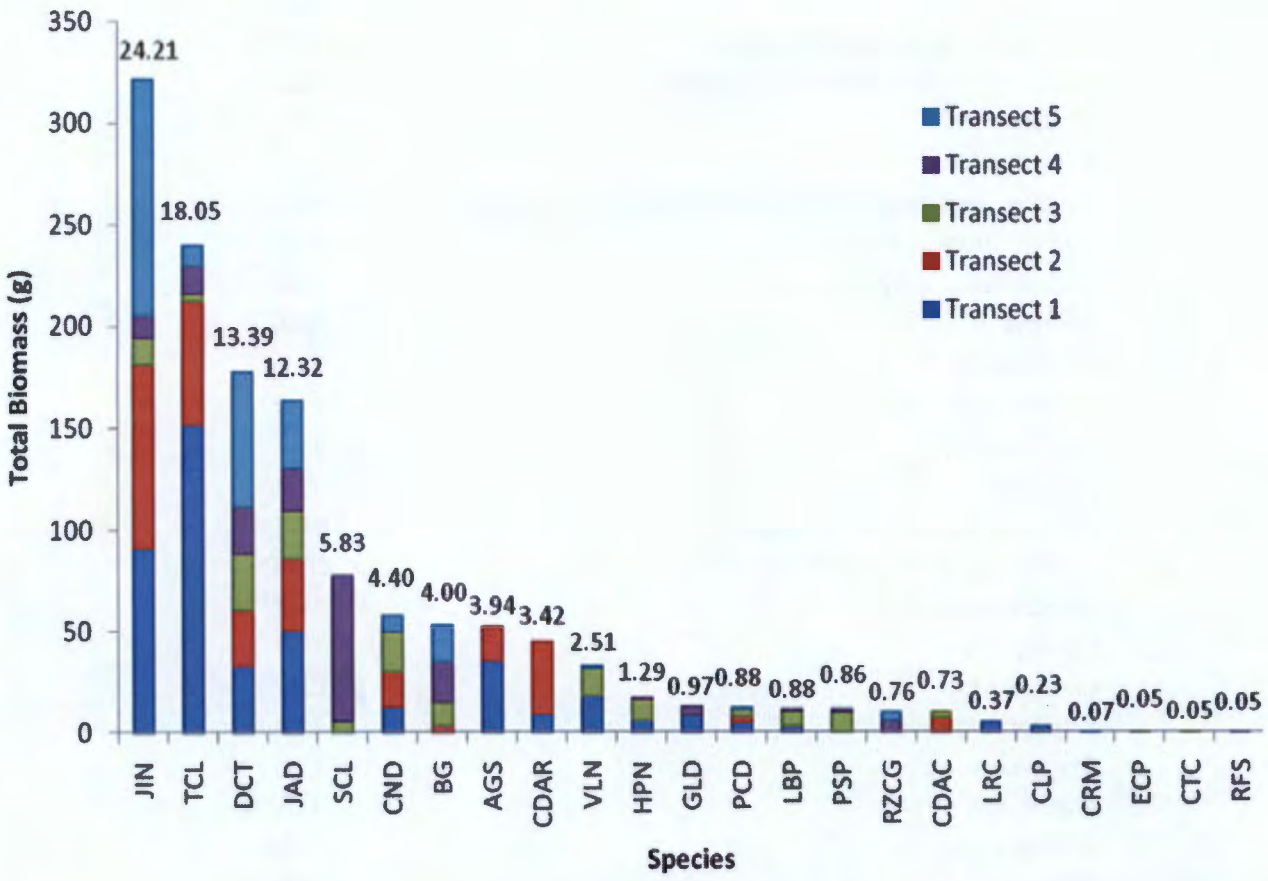


Figure 2. Total wet weights and percentages (mass-wise) of algal turf species found across the entire study site. Mass is plotted and percentages are indicated above each mass column. Columns are stacked according to amounts found in each transect. For species codes see Table 1.

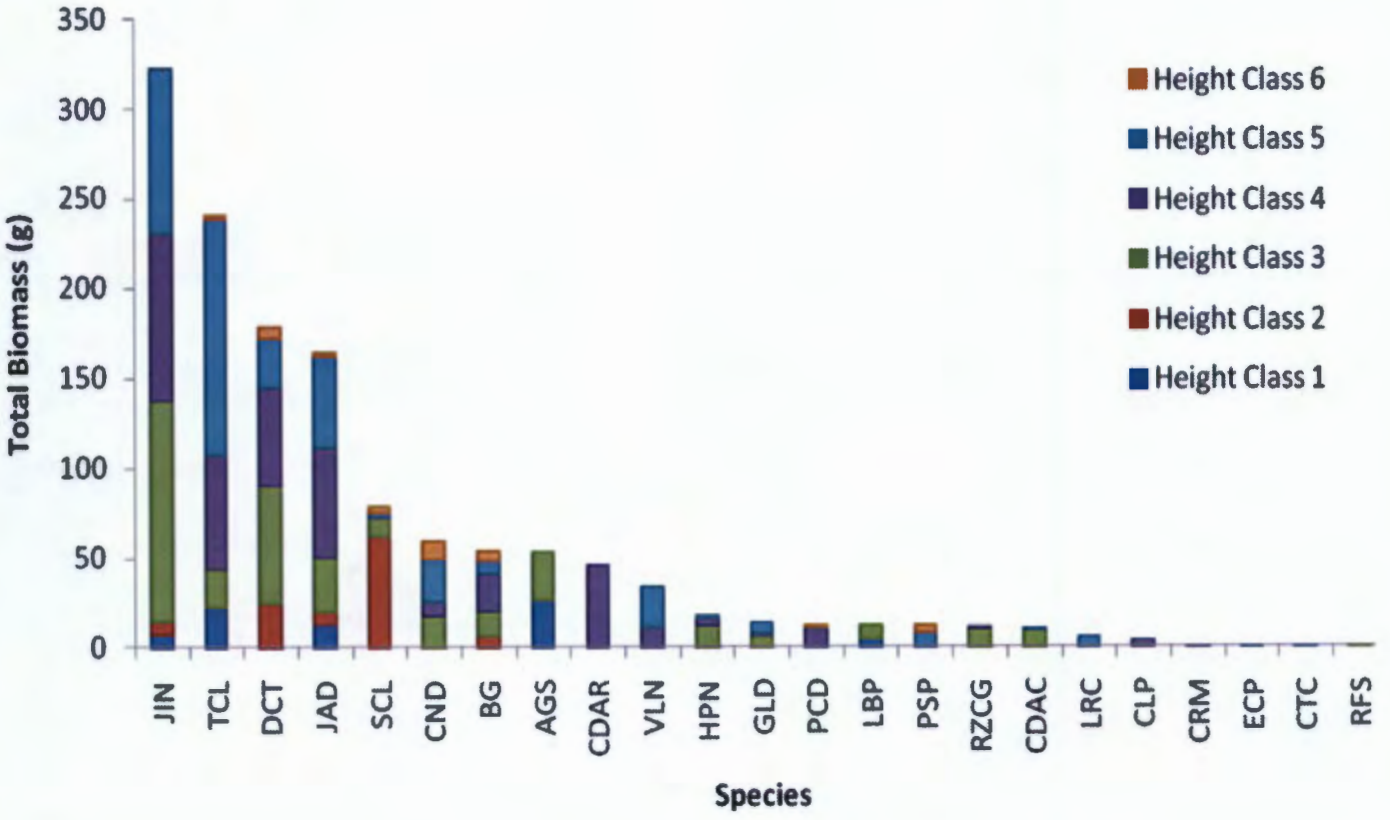


Figure 3. Total wet weights (g) of algal turf species collected across the entire study site. Columns are stacked according to the amount found in each height class. Height Class 1: 1-20 cm above CD; Height Class 2: 21-40 cm above CD; Height Class 3: 41-60 cm above CD; Height Class 4: 61-80 cm above CD; Height Class 5: 81-100 cm above CD; Height Class 6: 101-120 cm above CD.

Results of SIMPER analyses factored first by transect then by height class showed that *Tolypiocladia glomerulata*, *Jania intermedia*, *Jania adhaerens* and *Sphacelaria tribuloides* contributed the most towards similarities within both transects and height classes (Table 3). Tables 4 and 5 show that *J. intermedia*, *T. glomerulata* and *S. tribuloides* contributed the greatest to dissimilarities between transects, while *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Léon, *S.tribuloides*, *J. intermedia* and *T. glomerulata* contributed the most to dissimilarities between height classes. Interesting to note is that *J. intermedia* contributed the greatest to similarities within both Transects 2 and 5, as well as contributing the greatest to dissimilarities between both of these transects when compared to any others. The same pattern can be seen in the height classes with *S. tribuloides* showing the greatest contribution to similarity in Height Class 2, as well as contributing greatest to dissimilarities when Height Class 2 was involved in any comparisons. Though there was only one quadrat in Height Class 1 and therefore no similarity contribution data, it can still be seen that *A. taxiformis* only contributed towards dissimilarities when Height Class 1 was involved in the comparison. *A. taxiformis* was only found in three quadrats, two in Transect 1 and one in Transect 2 (See Figure 2), and in both transects

these were quadrats lower down on the shore (see Figure 3). Interestingly, though *A. taxiformis* is seen only in three quadrats, it contributes 3.94 % of the total algal mass collected, indicating that in the areas it is found in it is prolific. ANOSIM analyses indicated weak relationships between both transects (Global R = 0.38) and height classes (Global R = 0.21).

Table 3. Results of SIMPER analysis showing species contributions to similarities (Bray-Curtis) between quadrats within groups. Quadrats were grouped (factored) by transect as well as by height above Chart Datum.

Factor Groups	Species Contributing	% Contribution
Transect 1	*Tolypiocladia glomerulata*	60.66
Transect 2	*Jania intermedia*	33.09
Transect 3	*Jania adaerens*	28.96
Transect 4	*Sphacelaria tribuloides*	63.76
Transect 5	*Jania intermedia*	41.96
Height Class 1	N/A	N/A
Height Class 2	*Sphacelaria tribuloides*	73.43
Height Class 3	*Jania intermedia*	27.63
Height Class 4	*Jania adhaerens*	38.85
Height Class 5	*Tolypiocladia glomerulata*	36.06
Height Class 6	N/A	N/A

Table 4. Results of SIMPER analysis showing species contributions to dissimilarities (Bray-Curtis) between transects sampled.

Transects Compared	Species Contribution	% Contribution
Transects 1 & 2	*Jania intermedia*	25.61
Transects 1 & 3	*Tolypiocladia glomerulata*	30.55
Transects 2 & 3	*Jania intermedia*	23.34
Transects 1 & 4	*Tolypiocladia glomerulata*	28.75
Transects 2 & 4	*Jania intermedia*	21.58
Transects 3 & 4	*Sphacelaria tribuloides*	24.10
Transects 1 & 5	*Jania intermedia*	27.62
Transects 2 & 5	*Jania intermedia*	27.93
Transects 3 & 5	*Jania intermedia*	33.63
Transects 4 & 5	*Jania intermedia*	0.98

Table 5. Results of SIMPER analysis showing species contributions to dissimilarities (Bray-Curtis) between height classes of samples.

Height Classes Compared	Species Contribution	% Contribution
Classes 1 & 2	*Asparagopsis taxiformis.*	28.53
Classes 1 & 3	*Asparagopsis taxiformis.*	24.32
Classes 2 & 3	*Sphacelaria tribuloides*	22.25
Classes 1 & 4	*Asparagopsis taxiformis.*	28.46
Classes 2 & 4	*Sphacelaria tribuloides*	21.15
Classes 3 & 4	*Jania intermedia*	24.46
Classes 1 & 5	*Asparagopsis taxiformis.*	32.07
Classes 2 & 5	*Sphacelaria tribuloides*	23.91
Classes 3 & 5	*Jania intermedia*	24.08
Classes 4 & 5	*Jania intermedia*	22.59
Classes 1 & 6	*Asparagopsis taxiformis.*	26.57
Classes 2 & 6	*Sphacelaria tribuloides*	28.19
Classes 3 & 6	*Jania intermedia*	22.90
Classes 4 & 6	*Jania intermedia*	18.00
Classes 5 & 6	*Tolypiocladia glomerulata*	24.67

Figure 4. illustrates biomass patterns of the five greatest contributor species with height above CD. *T. glomerulata* shows the greatest biomass higher up on the shore, while *J. intermedia*, *S. tribuloides* and *A. taxiformis* all show the opposite pattern. *J. adhaerens* shows a slight increase in biomass with increasing height above CD. Figure 5. shows the same species as Figure 4 plotted against the amount of sediment found within each quadrat. The graphs show *T. glomerulata, J. adhaerens* and *A. taxiformis* to occur in greatest abundance where sediment mass is low, while *S.tribuloides* occurs more where sediment mass is higher. *J. intermedia* shows no distinct pattern and occurs over all sediment masses. The trends shown in Figures 4 and 5 are not statistically significant relationships, however, but we can see that there is some pattern emerging and further study with greater data sets may indicate significance in the relationships between species biomass and both height above CD and amount of sediment.

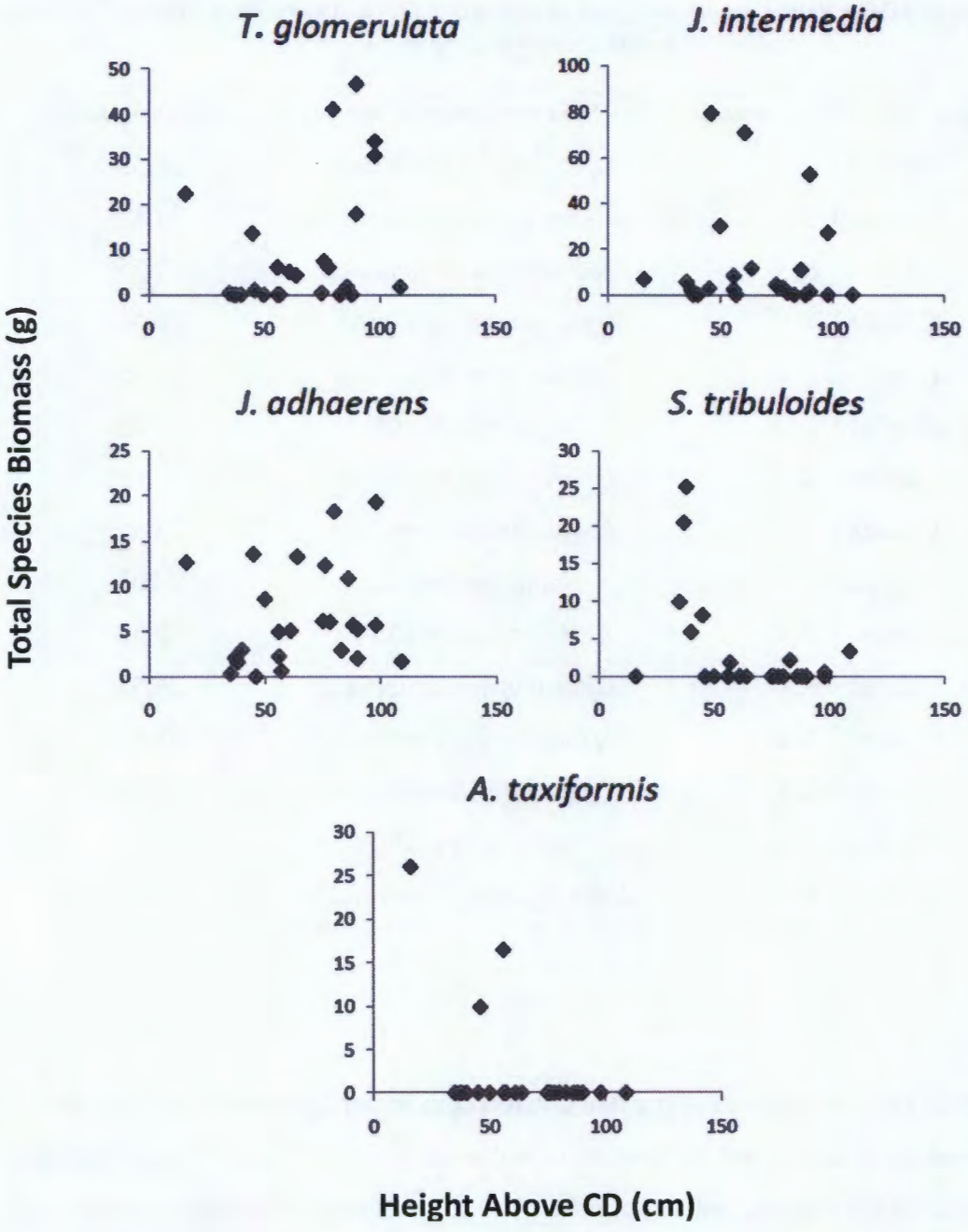


Figure 4. Graphs showing the five species contributing the most towards similarities between quadrats within samples and height classes as well as dissimilarities between both transects and height classes, plotted as biomass against height above Chart Datum so as to indicate each species' general occurrence pattern vertically along the shore.

CANOCO correlation analyses showed amount of sediment (sand) and height above CD (height) to be having almost opposite effects on the species found within the quadrats, as we can see that the sand and height vectors are pulling in almost opposite directions for both algal species and algal plus animal species data (Figures 6 and 7 respectively). Noticeable in both Figures 6 and 7 is the fact that samples from Transect 4 (T4Qx) are clustered together far along the sand vector, while samples from Transect 3 (T3Qx) are clustered far down the height axis. This suggests that quadrats found in Transect

4 are greatly affected by sand, while occurring lower down the shore, while quadrats form Transect 3 are greatly affected by height and are therefore found higher up on the shore and less affected by sediment. Most samples, however, are clustered towards the middle and no well defined patterns can be seen.

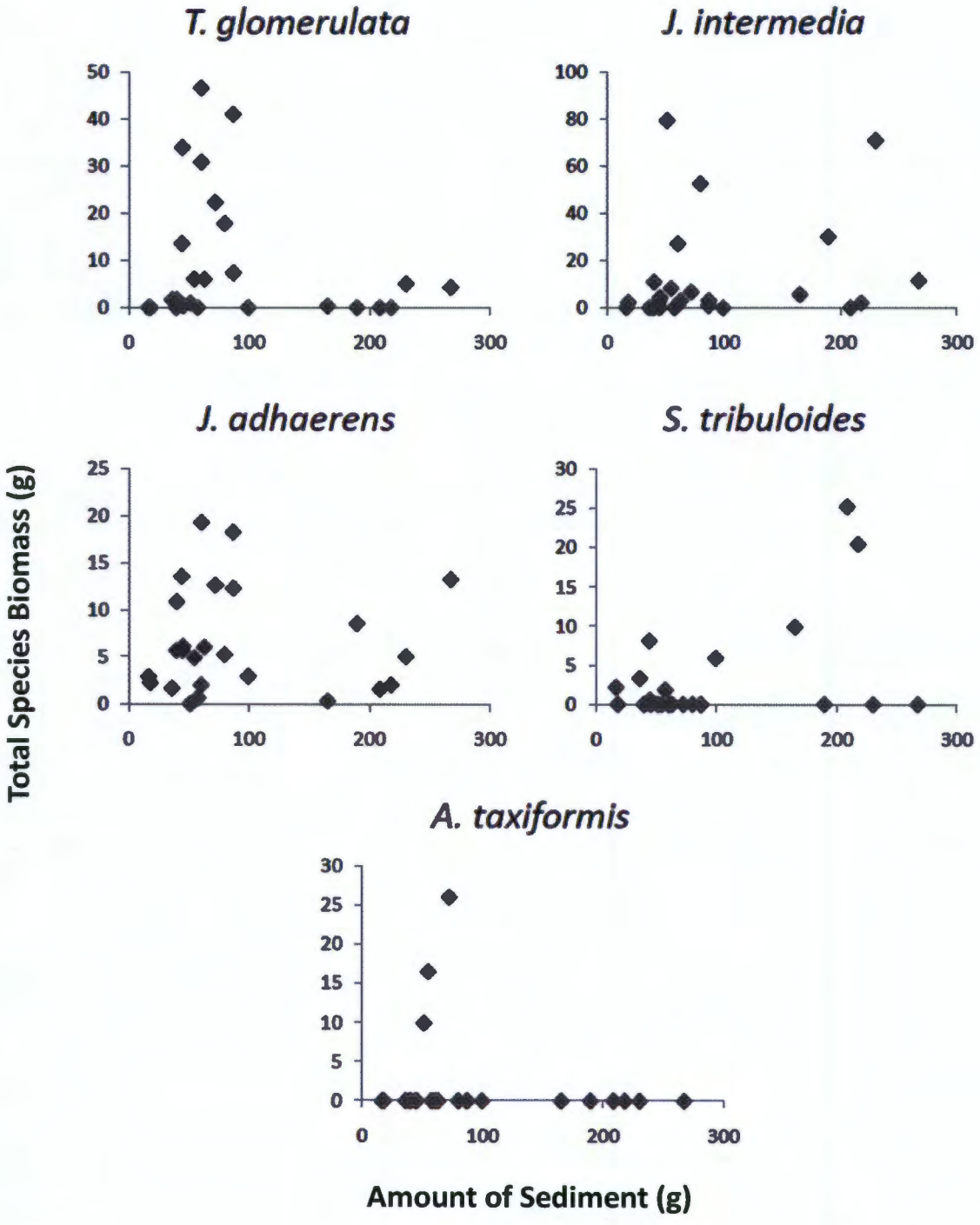


Figure 5. Graphs showing the five species contributing the most towards similarities between quadrats within samples and height classes as well as dissimilarities between both transects and height classes, plotted as biomass against amount of sediment so as to indicate how each species' general occurrence pattern may be affected by sand.

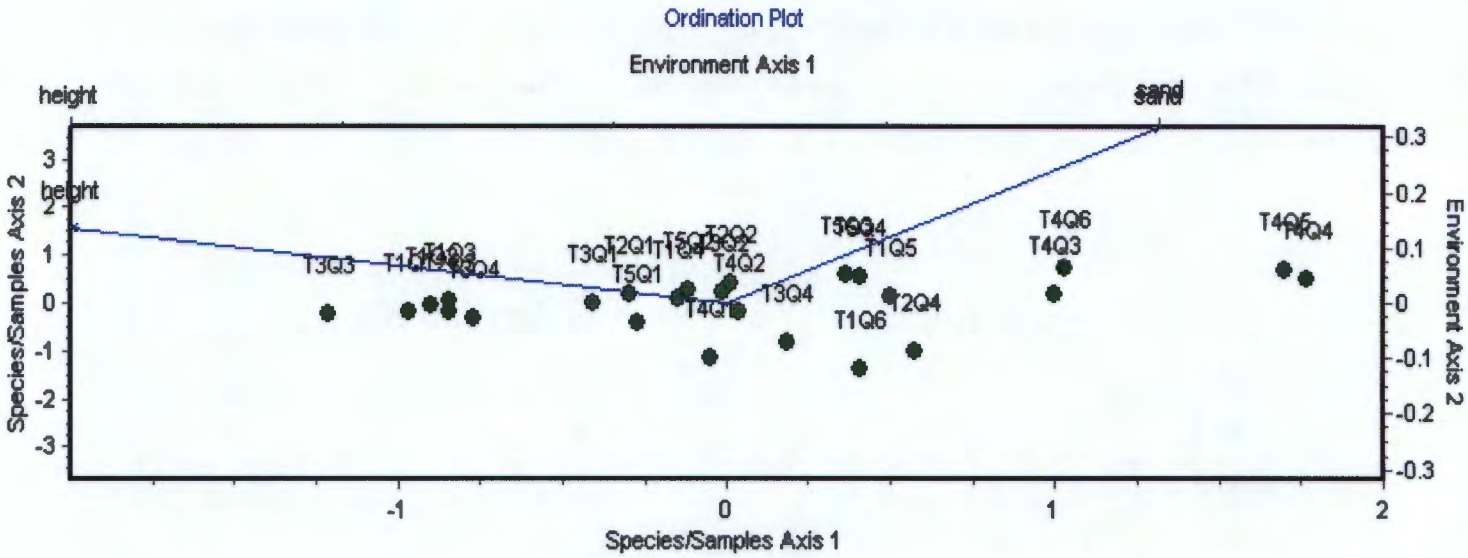


Figure 6. Canoco Correlation Analysis testing the effects of sand and height above CD as environmental factors acting on algal species within the samples. Analysis was performed using sites at species centroids.

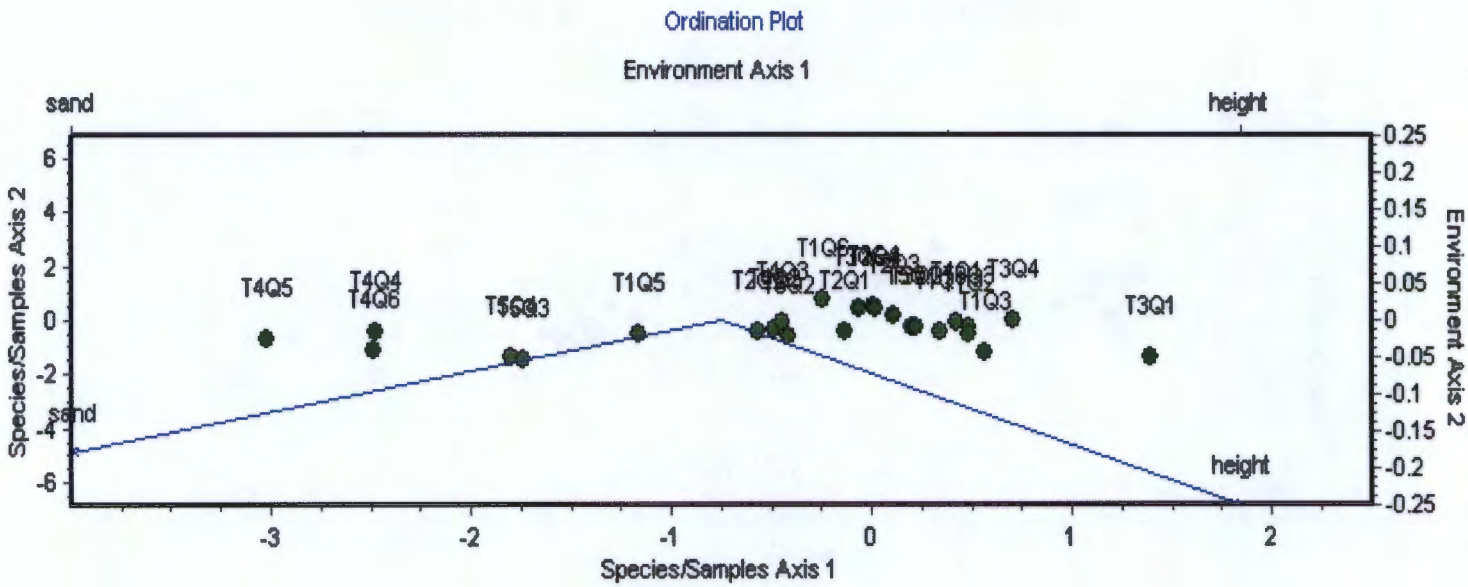


Figure 7. Canoco Correlation Analysis testing the effects of the sand and height above CD as environmental factors acting on all species (algal and animal) within the samples. Analysis was performed using sites at species centroids.

Average linkage analyses and MDS ordination plots of algal species indicated no very obvious patterns of clustering between the samples from each quadrat (Figures 8 and 9 respectively). In fact, Figures 8 and 9 show some discrepancies. Figure 8 indicates a close similarity between T4Q1 and T4Q3, though this is not seen in Figure 9. Figure 9 shows T1Q1, T1Q2 and T1Q3 closely clustered, but this is not matched in Figure 8, where the samples are clustered, but not as closely clustered as T4Q1 and T4Q3.

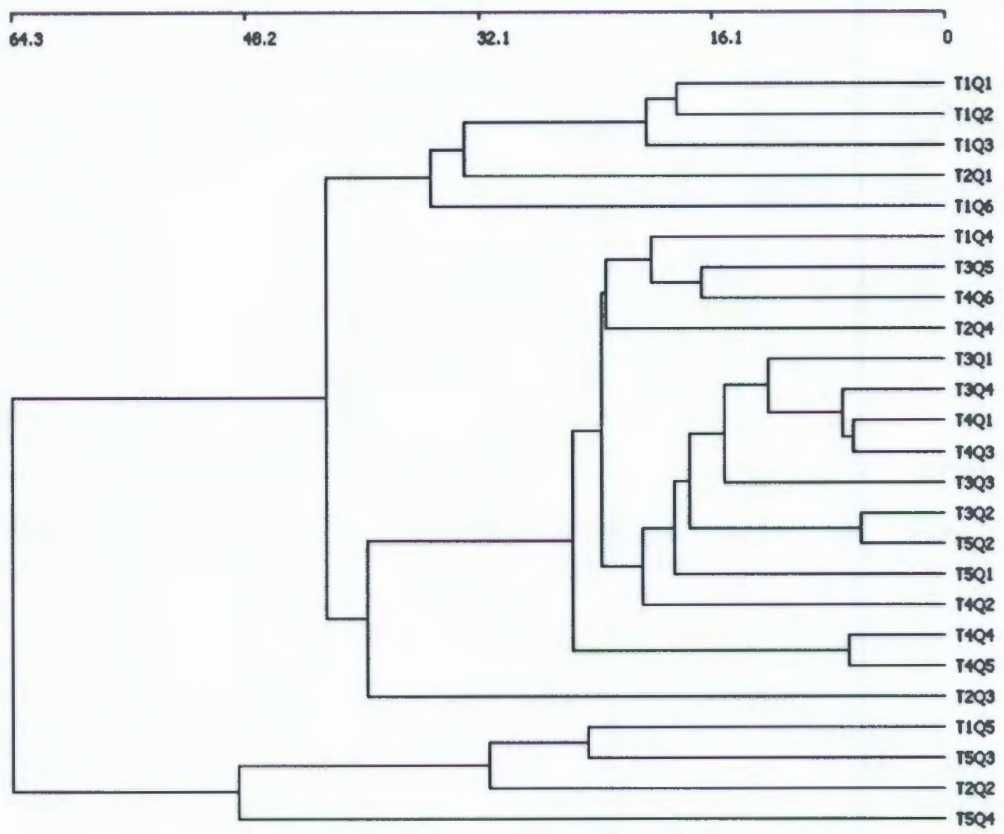


Figure 8. Average linkage analysis using Euclidean Distance as measurement showing similarities between algal species found within samples.

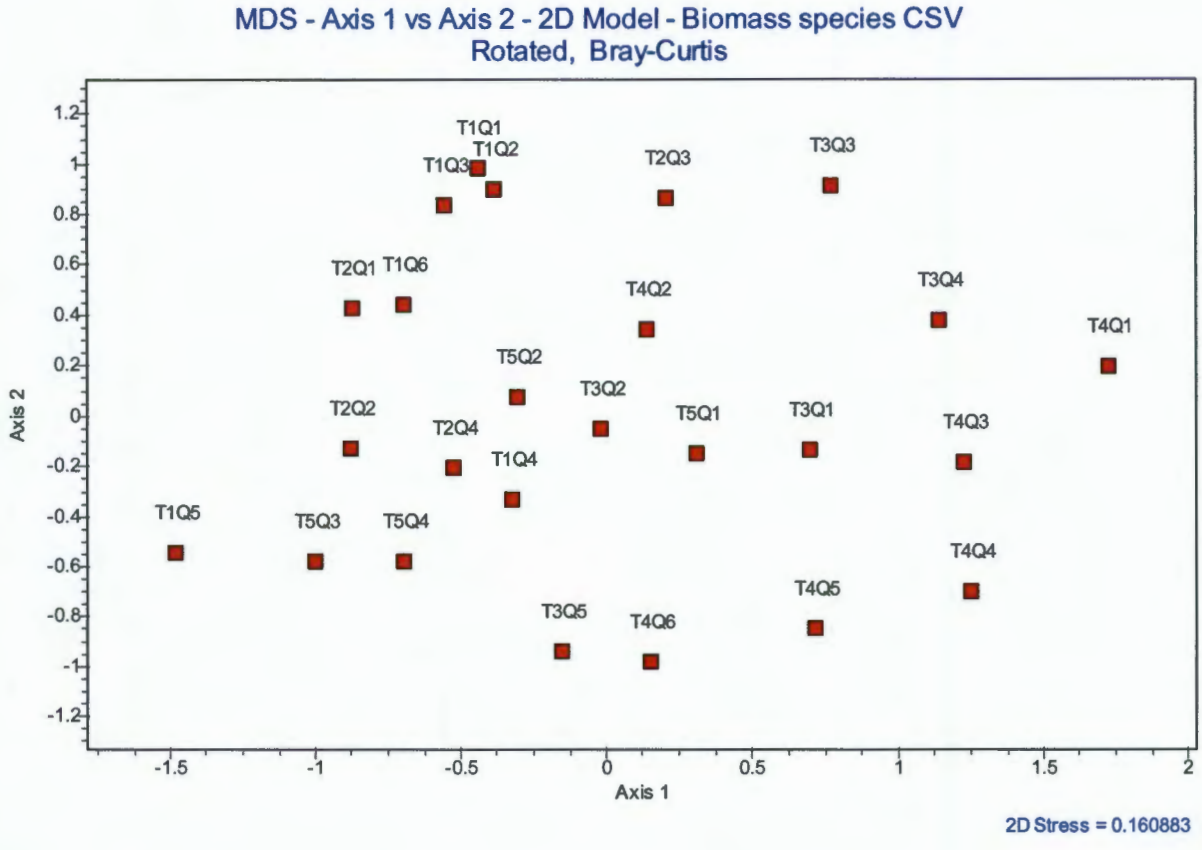


Figure 9. MDS plot showing Bray-Curtis similarity between algal species within samples.

Similar discrepancies between the average linkage and MDS plots are seen in the algal plus animal species average linkage and MDS ordination plots (Figures 10 and 11 respectively). In Figure 11 we see samples T5Q4 and T5Q3 clustered close together, but Figure 10 shows sample T5Q4 not clustered particularly closely to any other samples, while T5Q3 is clustered with T1Q5, which is quite a distance away in Figure 11. However, we do also see some agreement for some of the samples. Both plots show samples T1Q4 and T2Q4 closely related to one another and clustered far from all the other samples, and both plots show samples T3Q2 and T5Q2 closer to one another than to any other samples. While we see these small similarities between samples, there is no very distinguishable pattern seen in either the algal species or the algal plus animal species average linkage and MDS ordination plots.

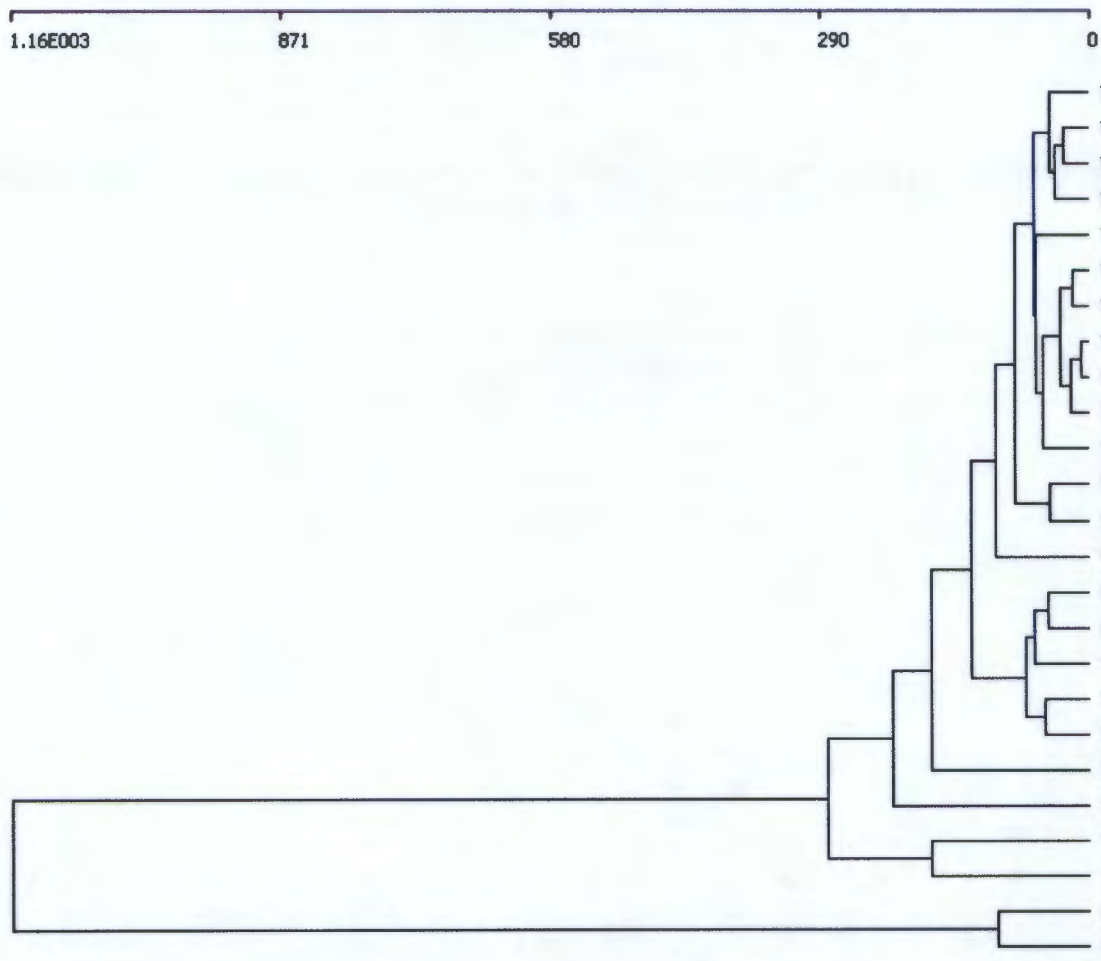


Figure 10. Average linkage analysis using Euclidean Distance showing similarities between all species (both algal and animal) found within samples.

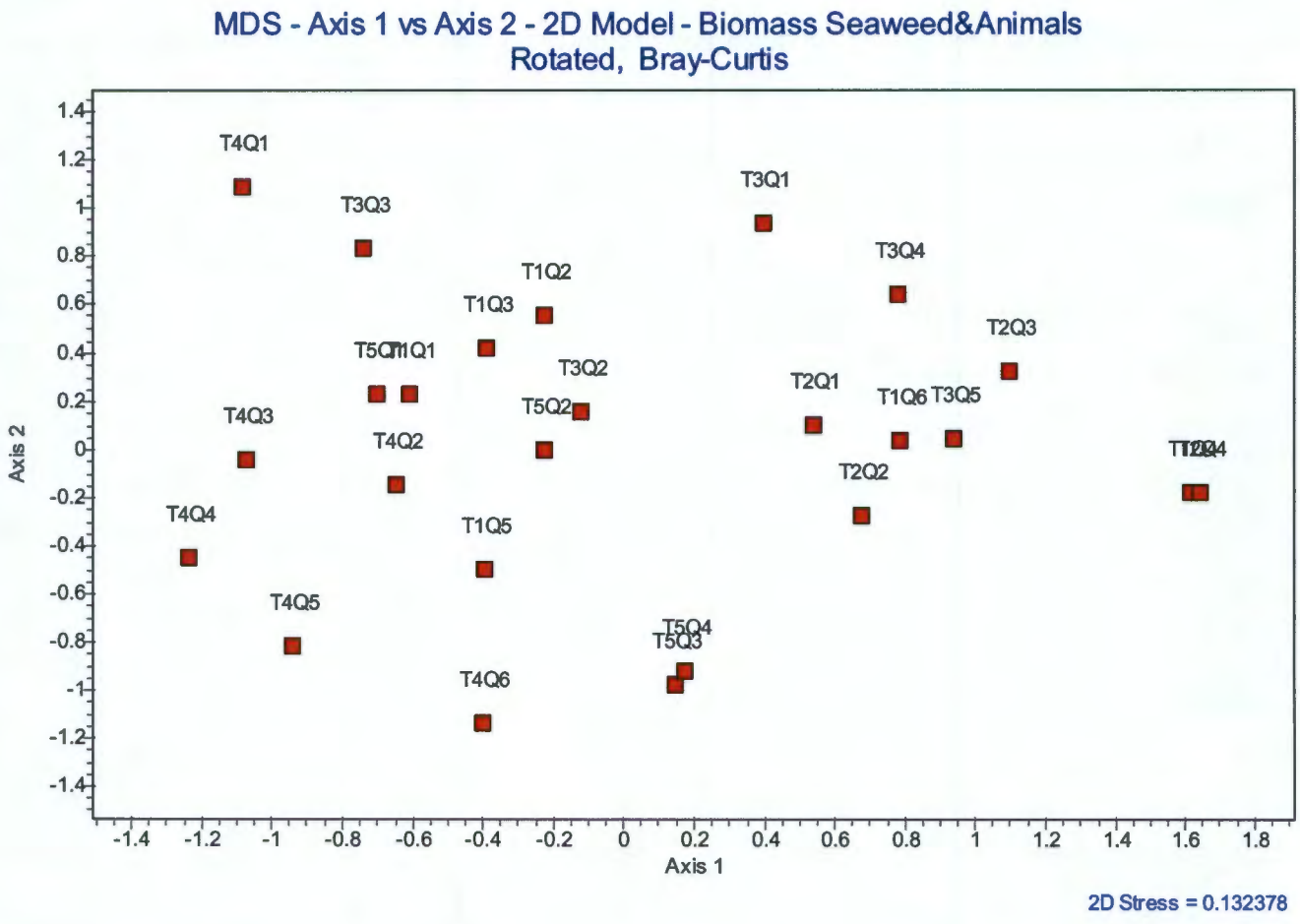


Figure 11. MDS plot showing Bray-Curtis similarities between all species (both algal and animal) within samples.

Results of a multiple regression performed on species richness (dependent), amount of sediment (predictor) and height above CD data (predictor) indicated no significant predictor relationships between any of these variables ($R^2 = 0.26$). Correlation coefficients calculated from the multiple regression are displayed in Table 6. All relationships found were non-significant.

Table 6. Correlation coefficients indicating the strengths of relationships between variables used in a multiple regression (Height above CD, Sand Wet Weight and Species Richness).

	Height above CD	Sand Wet Weight	Species Richness
Height above CD		-0.428	0.401
Sand Wet Weight	-0.428		-0.533
Species Richness	0.401	-0.533	

A nonparametric Kruskal-Wallis Multiple Comparisons analysis testing for significant differences in species richness between transects indicted that Transects 1 and 4 had significantly different species richness (Kruskal-Wallis (KW): $H = 14.57$, $p = 0.0057$; Multiple Comparisons (MC): $p = 0.021$), while all others were non-significant. The same test for differences in species richness between height classes indicated no significant differences between any of the height classes (KW: $H = 8.61$, $p = 0.126$). Kruskal-Wallis Multiple Comparisons tests performed on the amount of sediment found showed significant differences between Transects 3 and 4 (KW: $H = 13.98$, $p = 0.007$; MC: $p = 0.019$) as well as between Transects 3 and 5 (MC: $p = 0.008$), but no significant differences between height classes (KW: $H = 13.04$, $p = 0.023$). The same tests performed on the height above CD data indicated a significant difference between Transects 3 and 4 (KW: $H = 11.25$, $p = 0.024$) as well as significant differences between Height Classes 3 and 5 (KW: $H = 22.77$, $p = 0.000$; MC: $p = 0.034$) and between Height Classes 2 and 5 (MC: $p = 0.002$).

Discussion

Articulated coralline red algal species dominated the shore at Jesser Point, with the two species we found there, *J. intermedia* and *J. adhaerens* collectively accounting for 36.53 % of the total algal biomass collected. Interestingly, while Figure 4 indicates greater individual biomass points lower down on the shore for *J. intermedia* and *J. adhaerens*, Figure 3 shows that the greatest biomass to be found for both of these species occurs in Height Classes 3, 4 and 5 – between 41 and 100 cm above Chart Datum. This is not entirely in agreement with Wallenstein et al. (2009), who report that Neto & Tittley (1995) and Wallenstein et al. (2008) found that in the Azores coralline turf biomass increased towards the lower shore, while non-calcareous turfs were found to have a more even distribution across the shore. Lüning (1990) includes the Azores within the Warm-Temperate Atlantic Region and though the algae found there are mostly Lusitanic and Mediterranean species and therefore temperate, it is not uncommon for tropical algal species, as well as corals, to be found (Schmidt 1931). This may contribute to disagreement in zonation patterns between the algal species found at Sodwana Bay and those found in the Azores.

A. taxiformis was seen to contribute the greatest towards Bray-Curtis dissimilarities between Height Class 1 and any other height class compared to it (Table 3). Figure 4 shows that the greatest proportion of *A. taxiformis* biomass was found lower down on the shore, between zero and 60 cm above CD, while Figure 5 shows it to only occur in areas less affected by sediment. This indicates that *A. taxiformis* may be sensitive to both sediment loads and desiccation, explaining its distribution pattern low down on the intertidal and in the shallow subtidal of tropical to warm temperate regions (De

Clerck et al. 2005). *S. tribuloides* showed its greatest biomass in both Transect 4 and Height Class 2 (Figures 2 and 3 respectively), also contributing to the main Bray-Curtis similarities between quadrats for both these factor groups (Table 3) as well as contributing the greatest towards differences found between Height Class 2 and all others (Table 5). Transect 4 showed the highest amount of sediment (see Appendix) as well as the greatest mass of *S.tribuloides* indicating a possible positive correlation between the two (see Figure 5), though no statistically significant correlation was found ($R^2 = 0.216$). Interestingly, the Guide to the Seaweeds of KwaZulu Natal (De Clerck et al.2005 being the most recent volume) gives no mention to the genus *Sphacelaria* for KwaZulu Natal, the implications of which include the importance of investigation of all macroscopic seaweeds in studying and determining the algal diversity of a region.

CANOCO analyses indicate amount of sediment and height above CD vectors pulling in almost opposite directions, indicating that species affected more by height above CD are less affected by sand and vice versa. One would expect, from this, to then find a negative relationship between height above CD and amount of sediment, though this was not the case as no statistical relationship could be found. The fact that there isn't a strong pattern shown in the CANOCO plots indicates that neither factor is having significant effects on the community as a whole, supporting the fact that no relationship could be found. What is noticeable from the CANOCOs is that sediment is affecting a few of the quadrats quite heavily, namely those of Transect 4, which supports the pattern shown in Figure 5 and discussed above.

No distinct patterns or clusters could be found in Euclidean Distance average linkage plots or Bray-Curtis MDS plots. This indicates no significant relationships between the quadrat samples, also indicating no significant relationships between transects and height classes. Significant differences in species richness were found between Transects 1 and 4, with Transect 1 showing greater species richness than Transect 4. Regarding amount of sediment both Transects 4 and 5 had significantly greater amounts of sand than Transect 3, while the height classes showed no significant differences. Significant differences were found between Transects 3 and 4 regarding height above CD, with Transect 3 being significantly higher than Transect 4. Quadrats in Height Class 5 showed significant differences to those found in either Height Classes 2 or 3, with Height Classes 2 and 3 both being significantly higher than Height Class 5. However, results of a multiple regression between species richness, height above CD and amount of sediment indicated no predictive relationships between the three variables. Results of previous analyses of biodiversity and biomass patterns of subtidal algal turfs (Anderson et al. 2005) have shown both species diversity and biomass to decrease with increasing depth, and while sediment affected community composition, it showed no patterns with depth. Our

results agree to some extent in that there is no pattern seen between sediment and height above CD, though we do see slight differences in community composition, particularly with regards to *S. tribuloides*. Differences seen between transects regarding sediment content may be explained by the positions of transects along the shore. Both Transects 4 and 5 were situated in areas more sheltered from wave action thereby allowing the build-up of sediment without removal by strong wave action.

Scale plays an important role in ecology, as it affects both the ability to measure phenomena as well as perceived causes (Liuzzi & Gappa 2008). Assemblages of algal turf have been shown to be highly dynamic and variable both spatially and temporally (Coleman 2002). Spatial and temporal variation may occur as a result of various factors or combinations thereof, such as differences between pre-recruitment, recruitment or post-recruitment processes (Coleman 2002) that may occur at different spatial or temporal scales. It is very important to understand both the processes and interactions between them in order to understand patterns of spatial and temporal variability within algal assemblages (Coleman 2002). Spatial scales range from hundreds of kilometres, affected by global climate fluctuations and oceanographic currents (Cruz-Motta 2007), down to tens of centimetres affected by processes such as competition, predation and local water quality (Cruz-Motta 2007, Haas et al. 2009), down to less than tens of centimetres for smaller macroorganisms such as turfing algae. Temporal scales range from days to months to seasons to years (El Niño: Cruz-Motta 2007). The fact that all sampling was done at once during late summer means that the results shown here do not indicate temporal variation. This means it is possible that there is an unknown seasonal component, which may affect community composition or zonation patterns, not being seen in this study.

In recent years there has been an increase in turf coverage of reefs especially in urban areas, where changes in water quality as a result of human-induced sedimentation and input of nutrients result in loss of algal canopy species or corals (Tuya & Haroun 2006; Cruz-Motta 2007; Copertino et al. 2009; Haas et al. 2009). In order to more completely understand the effects of biotic and abiotic factors on algal turfs, as well as algal turfs on their environment and other species, understanding the scale at which effects occur and how they interact with one another is of paramount importance.

Conclusion

Algal turf has previously been labelled an autogenic ecosystem engineer (Liuzzi & Gappa 2008), modifying its environment to the point where it eventually creates its own ecosystem (Wallenstein et al. 2009). This may be what is occurring in the intertidal algal turf at Sodwana Bay. No desiccation gradients were seen vertically long the shore in terms of species composition and biomass patterns,

leading us to postulate that this may be a result of the algal turf creating its own microhabitat by trapping water, thereby preventing desiccation gradients from forming by remaining permanently damp, regardless of the ~1.5 m vertical distance between the bottom and the top of the shore. The maximum tidal range in South Africa is ~2 m, therefore all sampling took place between the low and high water limits. The lack of vertical zonation over the vertical range studied (1.2 m) illustrates the possibility that turfs are able to survive comfortably throughout the range of tidal desiccation as they retain water and remain damp. Higher on the shore there is a marked end to the turf coverage, and though the actual height of the boundary was not measured it seems to be above the high water mark, indicating that, while turfs can withstand tidal desiccation stress, more intense desiccation is possibly detrimental and the turf community may not be able to survive extended dry periods. Sediment seems to affect the turfs at a smaller scale than that of the whole community, rather affecting community composition within smaller spatial scales (i.e. at the 25 cm x 25 cm quadrat scale), though no significant patterns could be found. This study highlights the autogenic ecosystem engineer traits of algal turfs by showing the lack of desiccation pattern across almost the entire maximum tidal range. Further study would be beneficial in investigating whether the same would be true on an intertidal shore with a greater tidal range.

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Table 2*. Heights above CD, wet weights of sediment and wet weights of animal species for all quadrats in Transects 1 and 2.

	T1Q1	T1Q2	T1Q3	T1Q4	T1Q5	T1Q6	T2Q1	T2Q2	T2Q3	T2Q4
Height above CD (cm)	98	90	80	76	46	16	98	90	78	56
Sand (g)	44.7	60.3	86.8	87	51.2	72	60.5	79.8	62.9	54.6
Tubeworms (g)	67.3	110.7	27.7	0	38.1	0	0	0	0	0
Barnacles (g)	0	28.8	28.5	0	0	0	6.8	0	0	0
Reef Worms (g)	0	23.3	0	1147.1	0	126.6	76.3	108	234	1244
Limpets (g)	0	0.6	0	6.2	0	0	5.5	0	0	0
Mussels (g)	0	0	0	0	0	0	0	0	0	0

Table 3*. Heights above CD, wet weights of sediment and wet weights of animal species for all quadrats in Transects 3, 4 and 5.

	T3Q1	T3Q2	T3Q3	T3Q4	T3Q5	T4Q1	T4Q2	T4Q3	T4Q4	T4Q5	T4Q6	T5Q1	T5Q2	T5Q3	T5Q4
Height above CD (cm)	109	86	88	83	56	57	45	40	38	37	35	75	64	61	50
Sand (g)	36.1	40.1	39.7	16.5	18	57.5	44.2	99.3	208.5	217.7	165	45.2	267.2	230.1	189.5
Tubeworms (g)	0	61.8	206.8	0	0	375.8	31.8	33.5	13.7	5.6	3.31	70	47.8	2	1
Barnacles (g)	158	6.7	18.6	15.2	2.9	42.4	0	0	0	0	0	8.7	0	0	0
Reef Worms (g)	46.1	29.6	0	108.7	148.6	0	0	0	0	0	0	0	16.9	0	0
Limpets (g)	1	18.2	4.5	41.7	3.2	0	0	0	0	0	0	0	0	0	0
Mussels (g)	0	0	0	0.6	0	0	0	0	0	0	0	0	3.9	0	0

*Tables split as data set was too large to fit on the page

Appendix

Table 1. Percentage cover values for algal species found in notable quantities in the intertidal at Sodwana Bay, South Africa

	T1Q1	T1Q2	T1Q3	T1Q4	T1Q5	T1Q6	T2Q1	T2Q2	T2Q3	T2Q4	T3Q1	T3Q2	T3Q3	T3Q4	T3Q5	T4Q1	T4Q2	T4Q3	T4Q4	T4Q5	T4Q6	T5Q1	T5Q2	T5Q3	T5Q4
TCL	60	70	45	12	1	30	40	17	10	11	5	5	0	0	0	0	25	0	0	0	1	1	12	5	0
JIN	0	2	1	5	80	9	35	50	5	15	0	32	0	0	5	0	5	0	0	7	17	12	32	70	35
JAD	10	3	20	20	0	17	25	5	10	9	5	32	22	20	5	5	25	25	5	7	1	17	37	5	10
CND	10	1	1	0	5	1	0	11	5	5	30	5	5	20	10	0	0	0	0	0	0	0	10	0	5
DCT	0	8	5	35	1	1	0	16	0	20	20	15	0	0	35	0	0	5	5	15	50	15	7	20	45
RZCG	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7	0	0	1	1	0	1	0	5
PCD	1	0	5	0	0	0	0	0	5	0	5	0	1	0	3	0	0	0	0	0	0	0	1	0	0
GLD	10	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	8	0	0	0	0	0	0	0	0
VLN	1	13	10	0	0	0	0	0	0	0	0	1	50	0	0	0	0	0	0	0	0	5	0	0	0
SCL	1	0	0	0	0	0	0	0	0	0	10	0	0	15	0	15	15	50	80	70	30	0	0	0	0
LRC	7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
HPN	0	1	0	8	0	1	0	0	0	0	0	0	1	0	22	5	0	0	0	0	0	0	0	0	0
CRM	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CDAR	0	0	0	15	0	0	0	0	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CLP	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AGS	0	0	0	0	10	35	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CDAC	0	0	0	0	1	0	0	1	0	10	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
LBP	0	0	0	0	0	5	0	0	0	0	0	0	0	0	15	10	0	0	0	0	0	0	0	0	0
PSP	0	0	0	0	0	0	0	0	0	0	10	0	10	30	0	10	0	0	0	0	0	0	0	0	0
ECP	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
CTC	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0
RFS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
BG	0	1	0	0	0	0	0	0	5	0	15	10	10	5	0	50	15	20	10	0	0	50	0	0	0
SB*	0	1	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

*SB represents the percentage cover of pieces of shell not attached to animals but too large for inclusion as sand. These values were not used in analyses as individual quantities were negligible in all but two samples.